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## Rhizophoraceae Mangrove family

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**HABITAT****Native Range**

*Rhizophora mangle* L., the red mangrove, is native to the tropical and subtropical coasts of America, West Africa and the Pacific Islands of Fiji, Tonga, and New Caledonia (fig. 1) (15). On the Pacific coast of North and South America it is found from Punta Malpelo, Peru ( $3^{\circ}40' S$ ), to Puerto Lobos, Mexico ( $30^{\circ}15' N$ ). On the Atlantic coast it grows from Santa Catarina state, Brazil ( $27^{\circ}30' S$ ), to the Florida peninsula ( $29^{\circ}N$ ) (76).

Red mangrove grows best in shallow, silty soils under the influence of salty or brackish tidal waters, and in areas protected from wave and ocean current activity but associated with abundant fresh water runoff and rainfall (16). However, the red mangrove also grows under a wide variety of conditions—from hard rock outcrops to silty deposits, and from areas inundated most of the year by fresh water to areas with soil salinities higher than 60 parts per thousand (10, 17, 39). It may grow in areas with or without freshwater runoff.

This species attains its highest structural development in riverine mangrove forests in regions not subjected to cyclonic storms (e.g., hurricanes). These forests occur along the margins and flood plains of rivers where there is abundant freshwater runoff and high nutrient input. Red mangrove is the dominant species in coastal fringe forests along protected shorelines with a pronounced berm (35).

**Climate**

Red mangrove grows in tropical and subtropical dry, moist, and wet forest life zones. The best structural development is attained under conditions typical of the tropical wet forest life zone (66). It is found under a wide range of precipitation regimes (from below 800 to 10,000 mm per year) but is restricted to average temperature regimes of 21 to 30°C. The species is frost sensitive (72).

**Soils and Topography**

Red mangroves respond strongly to changes in microtopography and to changes in factors such as ground-water level, soil drainage, and soil salinity.

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Trees grow best in the lowest parts of swales, where water is always in motion, and in soils with a high degree of water saturation and high frequency and intensity of tidal inundations (66). In Jamaica, red mangrove occupies soils inundated by 520 to 700 tides per year (14).

Soils formed under red mangroves are sometimes characterized by high pH, high carbon to nitrogen ratios, and high contents of oxidizable sulfur, nitrogen, phosphorus, and carbon (27, 70). These soils become intensely acid on drying when they are reclaimed for agricultural purposes. Neutralization of the acid with lime or calcium carbonate is prohibitively expensive. Leaching of the acid by rainfall or seawater can take several years (30, 71).

**Associated Forest Cover**

As a component of mangrove communities, red mangrove is usually associated with other mangrove species such as *Avicennia tonduzzi* Moldenke, *A. bicolor* Standley, *A. germinans* (L.) Bl., *A. schaueriana* Stapt & Leechm, *Laguncularia racemosa* Gaertn, *Pelliciera rhizophorae* Tr. & Pl., and *Rhizophora harrisonii* Leechm.



Figure 1.—Distribution of *Rhizophora mangle* in the New World.

## LIFE HISTORY

### Reproduction and Early Growth

**Flowering and Fruiting.**—Flowers occur in single reproductive axes that originate on the terminal portion of branches, in the axil of a leaf pair. Each axis supports a modified dichasium that holds three to four flowers. The yellow or yellowish-white flowers are small, each with four persistent sepals, four ephemeral petals, eight stamens, and an inferior ovary with four ovules, only one of which usually develops (21, 74).

Pollen appears to be spread mainly by wind (67). After fertilization, the embryo continues its development without a detectable dormancy phase. Germination occurs when the embryo reaches a length of about 1.8 cm. After approximately 30 days the radicle protrudes through the fruit wall (31). The process of germination occurs while the embryo is still enclosed in the fruit and attached to the parent plant, a phenomenon typical of viviparous species (64).

**Seedling Development.**—After breaking through the fruit wall, seedlings grow for approximately 3 to 6 months before dropping from the parent tree (19). Fully developed seedlings are rod shaped, elongated, and composed of two parts, a short plumule that consists of a pair of stipules protecting the first pair of leaves and a long, heavy hypocotyl composed mainly of endospermatic aerenchyma tissue (31).

Wide variability exists in the size and weight of the mature seedling. This seems to be associated with the vigor of the parent tree. Propagules from dwarf forests average 10 cm in length, whereas those in riverine forests average about 25 cm. Davis (19) reported that an average tree in south Florida produced over 300 seedlings during one summer season.

Fallen propagules are transported by tidal currents (7, 51). Seedlings remain viable for long periods of time and are able to become established after floating for up to 12 months (19). The establishment of a seedling begins when it is stranded on shallow bottoms, and primary roots anchor the seedling. Less than 2 weeks is necessary for a seedling to become firmly anchored (51).

Densities of established seedlings vary from 0 to 2.4/m<sup>2</sup> in Biscayne Bay, Florida (4), to 0.6/m<sup>2</sup> in a basin forest in south Florida (36). A natural establishment rate of 0.1 seedlings/m<sup>2</sup>·yr has been reported (6).

Anchoring of the seedling seems to be a critical step in the process of establishment. In a planting experiment, 96 percent of the planted seedlings that were not staked were washed away by tide and wave action. In plots where the seedlings were staked, 93 percent survived (58). Beside tide and wave action, soil salinities higher than 60 parts per thousand generally prevent seedling growth, and salinities higher than 35 parts per thousand suppress structural development (16).

Rabinowitz (52) calculated a half-life of 338 days for cohorts of the species. Mortality rates are espe-

cially high in the early days of establishment as well as in saplings about 1 m tall (36). Competition in dense thickets of saplings could be responsible, although physiological mechanisms could also be involved.

**Vegetative Reproduction.**—Even though red mangrove sprouts to a certain extent when young, the coppice system is not recommended because of its lack of success (41). Air-layering techniques have been tried on this species and root development was observed 5 to 6 months after the plants were layered (12).

### Sapling and Pole Stage to Maturity

**Growth and Yield.**—Tree architecture follows the Attim's model characterized by axes with continuous growth, differentiated into a monopodial trunk and equivalent branches (26).

The growth rate and size attained by the trees depend largely on the characteristics of the growing site. In tropical areas red mangrove trees can attain heights of 40 to 50 m in humid riverine forests. These forests exhibit an aboveground biomass of up to 571 t/ha. Dwarf red mangrove forests growing in poor nutrient conditions have an aboveground biomass of about 17 t/ha and individuals grow to only 1 m in height (18).

Around the Caribbean, red mangrove forests rarely exceed 20 m and average between 10 to 15 m in height. In a random sample of 500 trees, 42 percent were 9.5 to 13.4 m tall and 12 to 15.5 cm in diameter at breast height (d.b.h.). Another 42 percent were 5.5 to 9.4 m tall and had d.b.h. values of 8.1 to 9.6 cm. The remaining 16 percent were 3.5 to 5.4 tall and had an average d.b.h. of 6.1 cm (3).

Growth rates are not available. Five-year-old stands in Trinidad attained an average height of 7 m and a d.b.h. of 6 cm (40). A red mangrove stand in Florida had a gross photosynthetic rate of 6.7 gC/m<sup>2</sup>·day, a 24-hr respiration rate of 1.9 gC/m<sup>2</sup>·day, and a transpiration rate of 2.57 mm/day (37). Net primary productivity rates ranging from 0.25 to 5.7 gC/m<sup>2</sup>·day have been measured in stands growing on low chlorinity waters (5 to 16 parts per thousand) (13). Annual wood production rates of 0.8 g/m<sup>2</sup>·day have been measured in Puerto Rican red mangroves (23).

In related mangrove species of the Indo-Pacific, wood yields of about 232 m<sup>3</sup>/ha have been estimated for 25-year-old *Rhizophora* stands (20). However, bark volumes (up to 20 percent), defective trees, and unusable debris can reduce the yield by 40 percent (75). Total wood yield has declined from 299 t/ha in virgin stands to 136 to 158 t/ha in second rotation stands in Malaysia (65).

**Rooting Habit.**—During the juvenile stages, red mangroves develop a short-lived subsystem of primary terrestrial roots. The adult form, however, is characterized by a subsystem of arching aerial roots (prop roots) that emerge perpendicularly from the trunk (fig. 2). These roots penetrate shallowly in the ground and



Figure 2.—A mature *Rhizophora* mangle stand in the Caribbean island of Inagua.

produce an extensive capillary root system that produces a thick fibrous soil.

Even though prop roots are generally restricted to the lower section of the trunk, they can sometimes be found higher up on the trunk and on lateral branches (16). These prop roots are typical of species growing on soft, waterlogged soils. A lenticel system and aerenchyma tissue are responsible for the gas exchange in these roots when soil is flooded (22, 59). There may also be a mechanical function to prop roots that helps to anchor the tree in unstable soils (34). Prop roots are adventitious in origin and grow at an average rate of 3 mm/day (21). Prop roots account for 25 percent (116 t/ha) of the total above-ground biomass in a Panamanian red mangrove forest (24).

**Reaction to Competition.**—The species is considered to be extremely intolerant of shade, and seedlings generally die under the closed canopy of parent trees. Gaps in the canopy that permit light to filter through promote the growth of dense seedling stands. High root and leaf production values have been recorded under full-light conditions (7).

In areas of high precipitation and/or abundant runoff and low soil salinities, mangrove species inter-

mingle with species adapted to less saline conditions. Competition in these areas can result in the elimination of the mangrove species. Red mangrove exhibits its highest photosynthetic rates in areas where terrestrial runoff and tidal flushing are high (37). In poorly flushed areas, competition and physiological stress result in higher respiration rates and slower growth rates (35).

Silvicultural practices for this species are not well developed in the western hemisphere. In Venezuela, mangrove silviculture is being tried experimentally, utilizing parcels (20 by 300 m) oriented perpendicular to the water courses with a rotation of 30 years (40).

Planting of red mangrove has utilized recently fallen ripe seedlings that have been cast on the beach (58). Storage of the seedlings for several days is possible, but prompt planting reduces any risk of letting the seedlings dry out. The seedlings are first buried and then staked to prevent removal by tidal or wave activity. In some cases, trees 0.5 to 1.5 m tall have been transplanted successfully if small branches are pruned and trees are removed with a rootball diameter approximately half the tree height (49). Estimated costs for planting in the United States range from \$1,100 to \$16,000 per hectare, depending on the technique utilized and whether the seedlings are collected or purchased (33).

In Thailand, trees with diameters between 15 and 25 cm are harvested with a rotation period of 25 to 30 years (4, 5). Thinning results in increases in the average tree diameter. In one area with a low tree density, a mean annual increment of 0.7 cm was recorded. In crowded natural forests, the mean annual increment was 0.5 cm (73). Thinning is practiced using the "stick-system," which involves using a standard-length stick to determine spacing between trees (44). The normal length of the stick is 1.4 m from 10 to 15 years and 1.9 m at 20 years. A third stick-thinning at 25 years is no longer practiced (65).

Natural regeneration has given satisfactory results. Regeneration has been enhanced by thinning the canopy 2 to 3 years before clearcutting. Natural regeneration in previously cut plots may not be sufficient, and planting of seedlings may be required. From 1950 to 1960 most of the *Rhizophora* plantations in Matang, Malaysia, were regenerated naturally. But, for the period 1970 to 1979, more than 75 percent of the plantations have required planting. Reasons for the natural regeneration failure are unknown (65).

**Damaging Agents.**—The infection of red mangrove trees by the fungi *Cylindrocarpum didymum* (Hartig) Wollenw. has been reported in south Florida. The fungi produces a gall disease that results in malformations of the trunk and prop roots (47). In a few cases, heavily infested trees have been killed by the disease or other agents acting on weakened trees.

Two wood borers, *Poecilips rhizophorae* Hopkins and *Sphaeroma terebrans* Bate, are occasionally found on this species (77). Both invade the prop roots of trees growing along tidal channels. Reports of *S.*

*terebrans* causing extensive damage to mangroves of south Florida (53, 54) seem to have been overestimated (55).

Red mangrove is susceptible to certain herbicides and may be killed by low concentrations of auxin type herbicides that may disrupt osmoregulatory mechanisms (69). Freshly established seedlings can be attacked by *P. rhizophorae* or eaten by crabs or monkeys (43, 50). Logging debris can obstruct natural regeneration or damage established seedlings (29).

## SPECIAL USES

Red mangrove is used as a source of fuel in most of the coastal towns of tropical America and West Africa. It is also a source of fence posts, stakes, poles, and railway ties. Posts and poles are reported as lasting 10 to 12 years (71). Poles respond adequately to impregnation treatments with pentachlorophenol and creosote. The sapwood portions tend to absorb creosote faster than the heartwood (63). Red mangrove responds adequately to treatments with copperized chromated borate and copperized chromated arsenite preservatives (32). Even though the wood is very resistant to fungal attack and termites, marine borers have caused extensive damage after exposure to seawater for 14 months (62). Good quality charcoal is also obtained from the wood. When burned, red mangrove yields approximately 60 to 65 percent of its weight as charcoal (63). Charcoal production of over 24,000 tonnes were reported for some plantations in Malaysia (16).

Red mangrove wood is also very dense. Arroyo (1) reported an average density of 1.03 g/cm<sup>3</sup> for dry wood. Chapman (16) reported a density of 1.08 g/cm<sup>3</sup> for sapwood and 1.15 g/cm<sup>3</sup> for heartwood. The wood has a high elasticity and hardness. It shows a tendency to crack and shrink in dry weather due to high volumetric contractions (16.8 percent) when going from green to dry wood (1). Red mangrove wood has potential use wherever high strength wood components are required.

The wood seems adequate for the production of dissolving pulp even though its use as a paper source seems to be precluded by the high thickness of the cell walls (41, 42). The durability of heartwood, combined with its hardness and strength, makes it a good raw material for both resin and cement-bonded particle board (63).

One of the main uses of this tree is the extraction of tannins from its bark. Bark yields for red mangrove trees in Nigeria are estimated as 110 to 130 t/ha (56). Tannin content of the bark ranges from 15 to 36 percent on a dry weight basis (16). Red mangrove bark is collected, dried, and pulverized to attain higher tannin yields (71). The bark is also utilized as a source of compounds for the preparation of phenolic adhesives (60). In West Africa and South America, red mangrove bark has been used for the medical treatment of bleeding, inflammations, diarrhea, and leprosy (45). Red mangrove leaves have been

suggested as a supplemental diet for cattle and poultry due to their high nutritional value (61).

It has been suggested that in shallow areas, red mangroves increase the natural rate of sedimentation by reducing waterflow velocity, trapping debris, and consolidating soft muds (11).

When growing in riverine conditions, red mangrove produces leaf litter at higher rates than most other mangrove species. Although rates of leaf litter production, accumulation, decomposition, and export to other ecosystems differ among the different types of forests (e.g., riverine, basin, fringe, dwarf), average annual leaf fall rates are remarkably constant; they were found to be 2 g/m<sup>2</sup>·day in the Caribbean region (35). The decomposition of this material provides food, nutrients, and substrate for many microorganisms. They constitute the beginning of a complex food web that includes many commercially important species of shrimp, crabs, and fishes (46). As part of the coastal complex, red mangroves maintain high rates of productivity, over 8 t/ha·yr, (37, 38) in estuarine zones. Some of these areas provide optimal conditions for the development of aquaculture enterprises (2, 48, 68).

## GENETICS

### Population Differences

The genus *Rhizophora* has been reviewed by Salvoza (57), Gregory (25), and Hou (28). Three species of *Rhizophora* (*R. harrisonii* Leechn., *R. mangle* L., and *R. racemosa* G.F.W. Mey.) have been reported for the American coasts. As a result of the varied conditions in which the plant grows, a high degree of population variation has been observed (57). This has resulted in a controversy over their taxonomic classification (8, 28).

Breteler (8, 9) proposed *R. harrisonii* as a hybrid between the other two American species. No clear morphological differences exist in North America's species of *Rhizophora* (9). Undoubtedly the subject requires further investigation.

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